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Neural and cognitive mechanisms underlying adaptation

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**General discussion
and future perspectives**

The main question posed in the introduction of this dissertation was:

“How does our brain adapt to and learn from our environment?”

One potential answer is that attention plays a key-role in the adaptation process and in learning, while factors such as reward provide the internal context guiding selective attention mechanisms towards relevant information, and away from irrelevant information. The studies reported in this dissertation have indeed shown that successful performance in terms of a fast and/or accurate response to an imminent important stimulus relies on selective attentional mechanisms. Moreover, we investigated the cognitive and neural mechanisms that are related to a change in priority of information in response to an external cue indicating the relevance of imminent information. In Chapter 3, for instance, the cue provided information about the possibility to obtain a monetary reward by responding quickly and accurately. Specifically, in the **first part** of this dissertation, we have shown that within a second after encountering a ‘potential reward’ cue, preparatory attentional brain mechanisms were recruited to change the state of the information processing system to be able to prioritize the reward related sources of information over others.

While these preparatory processes were dependent on information that was changing from trial-to-trial, task performance might also depend on information that requires the integration of information over multiple trials. In Chapter 4, for example, we studied whether individuals could learn to attend to and choose which categories of stimuli were more predictive of reward based on feedback information (i.e. positive [gains] and negative [losses] feedback) provided in a series of 20 trials. We have shown, in the **second part** of this dissertation, that when positive feedback is encountered during stimulus-reward learning, the priority of processing stimuli from the rewarded category is increased by activating the sensory brain regions that are specifically involved in processing the rewarded category.

In the remainder of this chapter I will discuss in more depth the neural and cognitive mechanisms that underlie adaptation as found in the studies in this dissertation. First, I will discuss the neural and cognitive mechanisms that predict successful behavior. Second, I will elaborate how we learn which stimuli are important to attend and respond to in our external environment. Third, I will discuss a theoretical model that can help to understand the relationship between attention, adaptation and their effect on learning. Fourth, I will outline the brain regions that are involved in these processes. Fifth, I will speculate about the underlying mechanisms by which the brain changes the priority of information (role of Alpha). Finally I will illustrate how attentional mechanisms might

change the processing of information over a lifespan.

Neural mechanisms that predict successful behavior

A crucial prerequisite for efficient or adequate behavioral performance is the ability to optimally prepare for the processing of an imminent target stimulus (target stimulus is broadly defined as any stimulus for which participant were instructed to do something with). Depending on the task, specific information in our internal and/or external environment is more important than other information. One key factor that impacts the importance of information is related to the potential for rewards, when potential is high, there is a good reason to try extra hard by placing demands on the internal system. When the potential for reward is low, there is no reason to do so. We hypothesize that if the importance of an event is made salient, such as by presenting a cue indicating that successful behavior in response to that event will be rewarded, the state of the information processing system would be modulated in preparation to optimally processes imminent information. The **first part** of the dissertation was mainly focused on modulation of the information processing system on a trial-to-trial or event-to-event basis. These studies (Chapter 2 and 3) revealed preparatory attentional mechanisms that can modulate the priority of the processing of certain information and subsequently facilitate the processing information, as shown by a relationship between preparatory attention and successful behavior (reflected in faster RTs).

To examine the effect of available cued information regarding a target stimulus on the preparation of the information processing system we examined in the studies described in Chapter 2 and 3 the neural mechanisms underlying these processes. We focused in particular on examining the preparatory neural mechanisms as indicated by the slow wave, fronto-central contingent related negativity (CNV) and the amount of oscillatory posterior Alpha power (8 to 14Hz), both EEG phenomena were previously found to be related to preparation (Grent-'t-Jong et al., 2011; Worden et al., 2000a).

In Chapter 2 we first investigated the trial-by-trial relationship between performance and variability in preparatory mechanisms. In particular, both CNV amplitude and Alpha power were measured on each single trial prior to the onset of the target stimulus, a visual search array (-700ms until search array onset). These indices were subsequently correlated with single trial behavioral performance. Results revealed that successful behavior as indicated by a relatively fast versus slow RT, was preceded by both an increase of the CNV amplitude and smaller prestimulus Alpha power.

In Chapter 3 we measured the same preparatory mechanisms, but in this study, we explicitly modulated the importance of successful behavior by offering monetary rewards in response to a fast and accurate performance. Subsequently, we inspected how reward modulated the size of the CNV and the power of Alpha oscillations. Results

revealed that when participants were offered monetary rewards they showed faster behavioral responses and an increase in the size of the cue-evoked CNV, as well as a decrease in posterior Alpha power.

CNV amplitude

The results from the studies in Chapter 2 and 3 of this dissertation support a link between the quality of behavioral performance to an imminent target and the amplitude of the CNV measured in the pre-stimulus interval. Brain activity reflected by the CNV has been suggested to originate from the slow-wave (<2Hz) fronto-parietal attentional-control network (Green et al., 2017; Grent-'t-Jong & Woldorff, 2007; Padmala & Pessoa, 2011). Grent-'t-Jong and Woldorff recorded high-temporal resolution EEG and high-spatial resolution fMRI while participants were either cued to prepare for an imminent target, or a control cue indicated that no target would be imminent. Using this preparation versus no preparation paradigm, EEG results revealed that in response to a cue that indicated an imminent target, the participant showed a CNV brain wave, whereas there was no CNV observed in response to a control cue. fMRI results of the same task revealed activation in both frontal and parietal areas for cued target versus control cue. Furthermore, previous studies have shown a link between hemodynamic activity extracted prior to the appearance of a target stimulus from the these fronto-parietal control areas and within-subject behavioral performance (Weissman et al., 2006). Regions of the attentional control network play an important role in the implementation of goal-directed behavior (reviewed in Corbetta & Shulman, 2002). The frontal regions seem especially important to keep task-goals active and maintaining a representation of the stimulus-response association (e.g. 'there will be an imminent Stroop stimulus for which I need to identify the word color by pressing the corresponding button on the keyboard!') (Miller & Cohen, 2001). The parietal regions are thought to be involved in coordinating what aspects of the external world to pay attention to (Ptak, 2012). That is, the parietal cortex seems to be an area involved in coding which aspects of the external world would benefit from attentional priority based on the product of encountered information (external) and internal demands.

Alpha power

Besides the CNV, we used Alpha-band power (8 to 14Hz) to investigate the relationship between preparation processes and subsequent behavior. Alpha is one of the most dominant brain waves in terms of oscillatory power. Importantly, the power in the Alpha frequency band has been found to have an inverse relationship with cortical activity as measured by the fMRI BOLD response (Scheeringa et al., 2012). Specifically, in this study by Scheeringa and colleagues, scalp recorded Alpha power was correlated with

the amount of deoxygenated blood in the posterior brain regions. Results revealed that when Alpha power was low there was more deoxygenated blood measured in these areas as compared to higher levels of Alpha power. In addition, ongoing fluctuations of Alpha power have been found to be inversely correlated with activity in the posterior sensory visual cortices including regions such as V1 and V2 involved in processing low-level features of visual information (Cichy, Pantazis, & Oliva, 2014; Petersson & Kleinschmidt, 2012; Scheeringa et al., 2012). Chapter 2 and 3 revealed that posterior Alpha power was linked to successful behavior in terms of RT performance. That is, fast RTs were preceded by lower prestimulus Alpha power as compared to slow RTs, similar to a previous finding linking lower Alpha power to the detection of imminent information (van Dijk, Schoffelen, Oostenveld, Jensen, et al., 2008a).

Mechanisms as reflected by the CNV and Alpha improve the processing of imminent information

The results of the studies described in this dissertation revealed that the preparatory mechanisms as reflected by the CNV and Alpha were related to successful behavior. We additionally observed that preparation, as reflected in pre-target changes of CNV and Alpha power, was related to changes in several ERP components that mark aspects in the cascade of processes underlying the processing of the imminent target. In particular, we were interested in the visual N1 elicited ~100 ms after stimulus presentation. The N1 is a component that is modulated by attention. That is, when participants are instructed to attend to certain stimulus properties, a larger amplitude of the N1 is seen when these properties are subsequently encountered (S. a Hillyard, Vogel, & Luck, 1998). Ongoing moment-to-moment fluctuations in both the CNV amplitude and Alpha power predicted (as measured by a correlation) the amplitude of the target evoked N1 indicating enhanced attention towards relevant information. Following the N1 effects, we found an improvement in several other attention-related cognitive functions, such as faster and improved attentional orientation towards and improved processing of the target stimulus. These studies show that preparation processes not only affects subsequent behavior in response to imminent target stimuli, but they also influence brain activity elicited by the processing of relevant task information.

CNV and Alpha power: independent phenomena?

The results from the studies in part 1 showed that both the amplitude of the CNV and the power of Alpha were related to successful behavior most likely via an effect on attentional mechanisms. However, the results also indicated that these indices of neural preparatory mechanisms operate independently of one another. Specifically, in Chapter 2, both the preparatory CNV amplitude and Alpha power correlated with the

amplitude of the search evoked N1 component, that did not correlate with one another. Further evidence comes from the study in Chapter 3: when cued with no-reward prospect, Alpha power did not vary, but the CNV did vary, as a function of whether or not the participant responded fast or slow on the imminent Stroop stimulus. In contrast, when cued with reward prospect, Alpha power did vary, but the CNV did not vary, as a function of whether or not the participant responded fast or slow on the imminent Stroop stimulus. This dichotomy suggests an interesting question: to what extent do the mechanisms reflected by the CNV and Alpha function independently?

What we know is that that CNV and Alpha effects originate from distinct cortical areas, because their topographical scalp distribution is highly dissociable (fronto-central versus posterior). It has been argued, however, that Alpha activity might be coordinated by the fronto-parietal control network, which, as discussed, has been understood as a source of the CNV (Grent-'t-Jong & Woldorff, 2007). Using repetitive Transcranial Magnetic Stimulation (rTMS). Capotosto and colleagues (2009) showed that applying a magnetic pulse to various regions of the fronto-parietal control network would disrupt the lowering of Alpha power in preparation of a target stimulus (Capotosto, Babiloni, Romani, & Corbetta, 2009). Based on these results, they suggested the fronto-parietal control network is involved in coordinating the reduction in Alpha over the posterior cortices.

Alternatively, based on the distinct scalp topography of the poster Alpha and fronto-central CNV effects in addition to independent relationships with stimulus processing (in particular the visual N1 ERP component), behavior, and, reward prospect we suggest that the amplitude of the CNV might reflect preparatory brain mechanisms related to higher level task-goals (e.g., keeping in mind that you are searching for the target stimulus on the left side) (Brunia et al., 2012; Gaillard, 1976; Marshall, O'Shea, Jensen, & Bergmann, 2015). In contrast, Alpha power, on the other hand, may reflect mechanisms tailored to sensory and stimulus or event specific preparation as illustrated by the studies in Chapter 2 through 4. Additional supporting evidence that Alpha is specific to stimulus feature specific preparation comes from other studies that have shown that the scalp topography of Alpha is specific to the cued modality (Straub, Wostmann, & Obleser, 2014).

Adaptation on a longer timescale: learning which stimuli are important in our environment

Adaptation of our information processing system might also occur on longer time scales compared to the adaptations from moment-to-moment we discussed in Part I of the dissertation. Especially in complex daily life situations efficient performance might depend on information that cannot be deduced from single events. For example,

information about stimulus probability might build up over trials, or even over a lifetime. The **second part** of this dissertation studied the neural processes that involved learning these regularities that requires the integration of information over a longer time-scale. For instance, this timescale could be tracking which stimulus is more predictive of rewards over a set of 20 (biased) coinflips. More specifically, when certain categories of stimuli are more predictive of rewards than others, adaptation involves learning to prioritize the processing of reward-associated stimuli by integrating information over multiple trials (**Chapter 4**). However, this time-scale could also be even much longer, such as is the case when learning which lines and combination of lines indicate a number or a letter. To study which brain mechanisms were related to learning we designed a probability learning task. Participants were presented with mini-blocks of 20 trials. On each trial, participants had to choose between either a face or a house. In each mini-block, either the face or the house was more likely to lead to a gain. Behaviorally, we showed that participants were able to learn in each 20-trial block whether the face or house was the more likely object to be rewarded.

Neurally, following a reward, we observed a relative decrease of Alpha power over stimulus-specific sensory areas involved in processing the rewarded stimuli compared to brain areas involved in the processing of task-irrelevant information. The study in Chapter 4 additionally showed that, after learning the stimulus-reward-association, an increased attentional bias was observed, as measured by the enhanced attention-related N2pc towards the reward-related stimulus category (Hickey et al., 2010b; Hickey & Van Zoest, 2012). Based on these findings we argued that changes in alpha power might reflect the modulation of the state of the system to increase the sensitivity of processing reward-related features in preparation for future encountered stimuli or events.

The stimulus category that has a higher probability to be rewarded, gains a higher priority of being processed over trials. These findings are in line with theories stating that our brain contains a stimulus priority map indicating a moment-by-moment representation of the priority of all features in the environment (Itti & Koch, 2000; Itti et al., 2001; Wolfe & Horowitz, 2004). These priority maps serve to guide attention towards task relevant information. We suggest that the updating of stimulus reward-associations through the stimulus priority map is related to Alpha power (I will discuss the nature by which Alpha can accomplish this feat further below), evidenced by the relationship between alpha power and attentional bias.

While this reward-based adaptation took place on a time-scale of minutes (20 trials), some adaptations are based on lifetime learning processes. The study described in Chapter 5 revealed that long term learning of letters and numbers resulted in the formation of specialized posterior neural pathways that can rapidly and without effort

process the learned information. More specifically, presenting strings of letters, numbers and false fonts to different age groups revealed differential developmental trajectories of the processing of letters and numbers. Note that the participants were passively viewing the screen during this experiment. The 7 and 10 year olds did not show an observable difference in electrical scalp recorded brain activity when processing letters versus numbers, whereas participants of the age of 15 and young adults showed a robust early lateralized difference in brain activity between letters and numbers (~150ms following the presentation of information).

In sum, in different studies we observed that available information about imminent stimuli guides our attentional system by efficiently tuning our information processing system towards task-relevant information either at the feature level (Alpha) or at a more general level (CNV). Moreover, adaptations of our information processing system might be implemented on a trial-by-trial basis, however, sometimes these changes might take years to be learned.

Theory underlying adaptation on different time-scales: from moment-to-moment adaptations to adaptation over a life-span

In Part 1 and Part 2 of this dissertation we studied adaptation as the change in responsiveness of those neural populations that were involved in processing an important event or stimulus. Theoretically, the relationship between adaptation and attention can be understood in the context of reduction of prediction space by means of attention (Feldman & Friston, 2010; Friston, 2010). The idea is that the brain constantly minimizes the possible range of predictions thereby limiting the amount of search possibilities in order to be efficient and to cope with limited processing capabilities. Dependent on the available resources the brain will adjust the thresholds of different regions to maximize or adapt its processing capabilities to different situations. For instance, when a cue predicts that a target will appear on the left rather than the right, the brain will reduce the prediction space by changing the processing state of those neurons involved in processing the left-visual field relative to the right one. If the uncertainty is higher, for example, when a cue does not indicate whether the target will appear in the left or right visual field but rather a general indication that a target is imminent, the brain will change the responsiveness of those neural responsiveness in both left and right visual fields, basically dividing the available resources over more options in this situation. The studies in this dissertation have shown that another key factor that can be incorporated into this theory is the behavioral relevance of information. That is, when something is

potentially rewarding, the brain can use this information to selectively recruit resources to influence the priority of processing the rewarding stimuli or eventThe process by which the brain adjust or tunes the neural connections could also be viewed as a process similar to backpropagation in artificial neural networks (Hagan, 2007; LeCun, Bengio, & Hinton, 2015). Artificial neural networks are computer simulated, and designed based on various properties of the human brain, they include individual neurons, connections between neurons and even different layers. The process of backpropagation is where artificial neural networks adjust connection weights between layers based on minimizing the loss function of the network, or the difference between expected and received input. This loss function can be viewed analogous to the prediction error that has been proposed to be elicited by brain elicits when encountering information such as feedback (René San Martín, 2012; W. Schultz, 2016). When the prediction error is zero, the network is perfectly tuned to that event. When the prediction error is not zero, the network is not optimized and could benefit from tuning based on available additional information. In the artificial neural networks the advantage of tuning connections with regard to search/ prediction space is clearly illustrated by having the network be trained using computerized versions of various games. In Chess for example, a recent study has played the neural network algorithm AlphaZero¹ (Silver, Hubert, et al., 2017; Silver, Schrittwieser, et al., 2017) against the best performing ‘brute force’² approach (e.g., such as the algorithm used by Stockfish, which can easily beat the best humans Chess players). Without knowing the rules, AlphaZero was able to learn the game within a day and beat Stockfish (Silver, Hubert, et al., 2017). Not only was the neural network able to win the Chess games easily, it required only 80 thousand possible solutions per move as opposed to the 70 million for Stockfish. This example clearly illustrate the fast reduction in prediction space that can be accomplished by optimizing an information processing system for a particular skill as humans do by using predictive information such as a cue or feedback.

Towards an integrative theory

In recent years several theories have come up with regard to the interaction between attention and rewards (Anderson, 2016, 2017b; W. Schultz, 2016). One of the most striking conclusions from these theories and the studies from this dissertation is the conclusion that attentional capture seems to be driven by rewards. For instance, in **Chapter 4** we have shown that Alpha power reflect those processes by which the brain prepares the sensory cortices for an important event or stimulus. These sensory brain regions have been hypothesized to play a key role in storing and learning which stimuli or events are

1 AlphaZero is a name of a deep learning computer algorithm and has nothing to do with the oscillatory Alpha extracted from EEG as studied in this dissertation.
2 Brute force is a computer method of finding a solution by inspection of all possible outcomes.

valuable and worth paying attention to (Anderson, 2016; Hopf et al., 2015; Schoenfeld, Hopf, Merkel, Heinze, & Hillyard, 2014). These preparatory processes, reflected by Alpha power, in turn enhance the processing of task relevant information resulting in responding fast and accurately or learning to choose a stimulus that has a high likelihood for obtaining a reward. However, to be able to modulate the sensory regions requires processes that can identify the value of specific stimuli or event and subsequently modulate activity in the sensory cortices. Based on the discussed research and available literature we can speculate about the functional role of some brain areas involved in the implementation of the processes underlying adaptation (**figure 1A & B**).

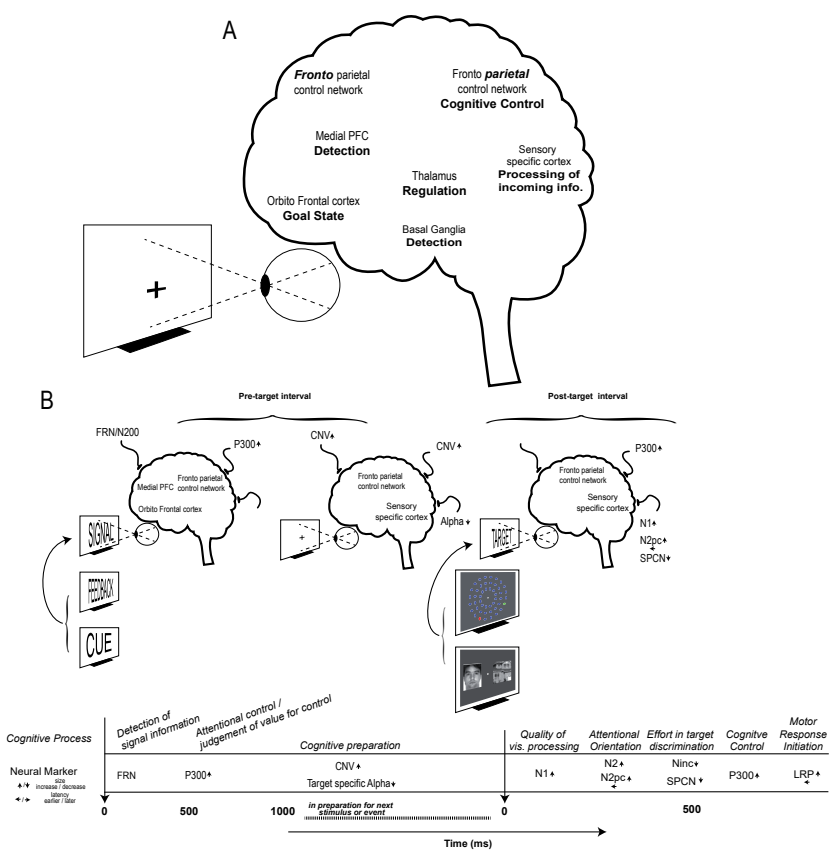


Figure 1. The brain contains various regions that are involved in adaptation and prioritization of certain information over others. (A) Regions that are related to specific sub processes necessary in adaptation. (B) Stages involved in adaptation. The brain detects the value of prioritization of an imminent stimulus or event. Detection is followed by a generic preparation (such as motor response preparation) and an adjustment of the threshold of the cortices involved in processing of the stimulus or event.

In the studies described in this dissertation we have used two types of stimuli that signaled information about the future; a cue stimulus and a feedback stimulus. Both stimuli provide information that can be used to adapt the information processing system in order to more efficiently process imminent information. In case of the cue stimulus, information is provided about imminent stimulus- or event-related characteristics, while feedback provides evaluative information about past performance that might be indicative of success of performance in the future. In **figure 1** no distinction is made between these two stimuli; both are regarded as a 'signal' that provides information that can be used to prepare for future actions and decisions.

The left side in **figure 1B** depicts the appearance of information presented to a participant. To be able to use that information to optimally prepare the information processing system, a number of processes can be discerned. The first processes in this cascade is the identification of the information provided. This identification process is not limited to extracting physical features of the information signal, but also includes the extraction of internal relevance of the signaled information. The identification and interpretation of the signal is followed by a functional implementation of this information in order to actually prepare for the upcoming event/stimulus. This involves tuning of the state of the system towards processing the signaled event/ stimulus with priority and to inhibit the processing of task irrelevant information (**figure 1B**, middle panel). Finally, the right panel of **figure 1B**, indicates those processes involved in the improvement of processing those stimuli or events that were signaled.

Directly following the detection of the signal that carries information about the future the task relevant information embedded in the cue or feedback stimulus needs to be extracted. For instance, when the signal is a reward there are several brain regions that have been found to show activation. Reward correlates in the brain have been found using both single unit recordings and fMRI, which have shown that several subcortical regions are responsive to explicit reward information. These regions include the ventral tegmental area (VTA), dopamine neurons in the substantia nigra, nucleus accumbens (NAcc), amygdala and (ventral) striatum (Adcock et al., 2006; Delgado, 2007; Floresco, 2015; W. Schultz, 2000b, 2015). These regions show increased activity when the participant is receiving a reward. Their responses are especially stronger relative to expectations given the current state of the system (reward prediction error - RPE). If the reward is equal to expected reward given the current state of the system, the RPE is zero, indicating that nothing in the system has to be changed (maintaining the status quo), when potential for reward is larger compared to expected reward, the RPE is greater than zero.

In addition, these subcortical regions have been found to be responsive when a stimulus or signal indicates a probability of gaining a future reward (Fiorillo, Tobler, & Schultz, 2003). These explicit subcortical reward-prediction signals are independent of the stimulus category and occur across multiple dimensions. It is however, not well known to what extent these signals are compared relative to the current state of the system (analogue to the reward-prediction error). One possibility would be that the activity in these neurons can explicitly code the difference in reward prospect given the current state of the system versus what could potentially be obtained (W. Schultz, 2016). In other words, when there is a signal that there is a possibility to obtain an imminent reward, activity in these regions indicate the importance to respond. Or activity in these regions could indicate if there is value in tuning the brain to obtain the reward as signaled by the prior event or stimulus.

Subcortical reward regions do not seem to work in isolation but rather in conjunction with cortical regions, especially areas in the medial prefrontal cortex (MPFC) (Botvinick, 2007; Bush et al., 2002; Klein-Flugge et al., 2016). Crucially, the activity from the medial prefrontal regions has been probed in this dissertation by inspecting the ERP component associated with MPFC activation, the feedback related negativity (FRN, peaking ~250ms following the reward/feedback). Activation in the MPFC varies according feedback, and especially the difference in value between the actual and the expected outcome, which is very similar to signals observed in the subcortical regions (i.e., reward-prediction error or RPE), as shown both in humans with functional MRI and in nonhuman primates with single-unit recording and also by studying the scalp recorded FRN ERP component (reviewed in San Martín, 2012; Tremblay, Hollerman, & Schultz, 1998).

Other factors to which the MPFC responds is the uncertainty, difficulty, and conflict in the environment (Kéri, Decety, Roland, & Gulyás, 2004). For instance, in another study (Mckay, Van Den Berg, & Woldorff, 2017) we explicitly modulated the both the difficulty and conflict in a stimulus discrimination task. In particular, we were interested to what extent the hallmark ERP component that is related to conflict detection and is manifested as a fronto-central negativity peaking around 450ms (the incongruency related negativity [Ninc] also known as the N450) was modulated by these two factors. The MPFC is thought to be the source of the Ninc (Liotti et al., 2000). Interestingly, we found a fronto-central negative deflection for both conflict and difficulty, which suggests that the MPFC has a much more general function. The function of the MPFC could perhaps be summarized as monitor of value for control (Shenhav, Cohen, & Botvinick, 2016). Value for control would refer to the integration process of the following information: reward prediction, calculating the amount of effort a task requires and finally, the costs associated when the effort is not spend.

Following the activity in the MPFC, the studies in Chapter 3 and 4 have revealed another potential marker for the internal value of control. More precisely, reward prospect and feedback loss information elicited a positive deflection, the P300 complex, which usually occurs around ~300ms following a stimulus. The neural source of the P300 is not well known, but is likely to include fronto-parietal control regions (Polich, 2012b). Although widely studied, the cognitive function of the P300 is ill defined and generally described as an enhancement in terms of cognitive resources (Nieuwenhuis et al., 2005; Polich, 2012a; René San Martín, 2012; René San Martín, Kwak, Pearson, Woldorff, & Huettel, 2016). Perhaps, rather than a general increase in cognitive resources, the P300 is a further reflection of value for control or perhaps “attention for reward”. For instance, in Chapter 3, following the reward-prospect cue there was a larger P300. In terms of internal demands a potential for reward could indicate that it is beneficial to pay close attention to the task and there is something to be gained, which specifically means that there is a value for control. In addition, in Chapter 4, following the FRN, a loss evoked a larger P300 compared to a gain. In terms of value for control, a loss could indicate that it is beneficial to pay close attention to the task and there is added information in the upcoming trials. In contrast, for a gain, there is less value for control because the stimulus that is most likely to yield a reward is already being chosen.

The studies in this dissertation have shown a crucial role for the visual posterior sensory cortices in facilitating the processing of imminent visual information. However, to be able to adapt these regions successfully, there has to be a mapping of stimulus or event value information to these early sensory regions. Previous studies have suggested that the orbital frontal cortex is a potential candidate to fulfil this role (FitzGerald et al., 2009; Leong et al., 2017; Y. Niv et al., 2015; Schuck, Cai, Wilson, & Niv, 2016; Schurmann, 2001; Sul et al., 2010; Wallis, 2011). For instance, Schuck and colleagues have shown that the orbitofrontal cortex shows task-specific activation. We suggest that when the subcortical regions, together with the MPFC, detect that there is potential for reward, the orbitofrontal cortex codes which task set is key to obtaining the reward. Importantly, to map the task set onto the relevant sensory regions the orbitofrontal cortex has fast number of connections to thalamic regions. The thalamus is a subcortical brain area located on top of the brainstem and has widespread projections from both subcortical reward sensitive regions as well as cortical frontal regions and projects to most sensory regions (Barbas & Zikopoulos, 2007; Parent & Hazrati, 1995). The connectivity between the orbitofrontal region and the thalamus make the orbitofrontal cortex a key region that could potentially orchestrate the sensitivity of task specific sensory regions through thalamic connections. This remains an open question that requires further investigation.

The role of Alpha oscillations in changing priority

As suggested in Chapter 2, 3 and 4, a functional interpretation of Alpha power is that it is a manifestation of adaptations in the brain, illustrating that the brain can learn which stimuli or events are behaviorally relevant and that this information can be used to optimize information processing. For instance, in Chapter 2, we saw that increases in Alpha power were related to a reduction in the quality of visual processes (smaller N1). In Chapter 3 we saw that reward-prospect influenced Alpha power which impacted the processing of imminent target stimuli. Finally, in Chapter 4 we found that Alpha was reduced over stimulus specific areas in response to a reward (i.e. when feedback was a gain) which subsequently altered the priority of processing the rewarded stimulus category. The neural origin of reductions in Alpha may be related to the thalamus. For instance, Scheeringa et al. (2016) found, using simultaneous EEG and fMRI recordings, that EEG Alpha rhythms mostly originated from the superficial and deep layers of the cortex which are well connected to the thalamus (Dantzer & Callaway, 2000). Functionally, a reduction in Alpha can be thought of as a reflection of mechanisms by which the brain is able to regulate information entering our information processing system through our senses (Benedek, Schickel, Jauk, Fink, & Neubauer, 2014; Bollimunta, Chen, Schroeder, & Ding, 2009; Dantzer & Callaway, 2000; Jensen & Mazaheri, 2010; Scheeringa, Koopmans, van Mourik, Jensen, & Norris, 2016) and thereby whether relevant information is actually processed while the processing of irrelevant information is actually inhibited.

A recent theory suggests that Alpha might coordinate cortical activity through a key biological mechanism called stochastic resonance (Lefebvre, Hutt, & Frohlich, 2017; Uzuntarla, Barreto, & Torres, 2017). Stochastic resonance is the mechanism by which random noise (random noise is always present in a biological large scale neural network) can amplify weak sub-threshold signals. In this theory, Alpha oscillations are an emergent property of the system, that is, neurons in the sensory system have a natural tendency to fire together between 8 and 12 times per second. Although, due to technological challenges, no studies have been able to prove to what extent individual neurons in the visual cortices actually entrain into the Alpha frequency, there is ample evidence that phase synchronization does occur in a wide variety of biological and non-biological non-linear systems (Strogatz & Goldenfeld, 2004).

The computation simulation by Lefebvre, Frohlich and Hutt (2017) showed that when the thalamus introduces noise in the cortical system, a lowering of Alpha power was observed, potentially induced by disrupting the entrainment or phase locking of neural oscillators (Kuramoto, 1975). Specifically, their model consisted of simulations of neural activity in terms of cortical pyramidal neurons and inhibitory neurons which had connections to the thalamus. Additionally, the results of the simulation suggested that

the likelihood of external input (such as a visual stimuli) to pass a threshold to induce local neural activity was dependent on the level of internal oscillatory activity in the Alpha band. Specifically, if Alpha power was high, stochastic resonance played a much smaller role (as there was less random noise), making it less likely for a weak external signal to pass a threshold. This is a key property in a system that needs to adapt to an ever changing environment. Because in situations of uncertainty or of potential reward, it is important to be able to assign a weight to certain brain areas. For instance, when a cue indicates an imminent target on the left side with 0.7 accuracy, it is still imperative to monitor the uncued location to avoid missing the target (Petersen & Posner, 2012; Stokes, Myers, Turnbull, & Nobre, 2014). As shown in Chapter 3 and 4, Alpha reduction can occur a moment-to-moment basis, but hypothetically, through physiological changes, this basic mechanism may also cause adaptation on much longer time-scales.

EEG Limitations and future directions

Part 1 and Part 2 of this dissertation showed that being able to adapt to an environment requires tuning the brain to prioritize processing those elements that are relevant. To study these processes we measured high-temporal resolution EEG. EEG is an incredibly powerful tool to study the cognitive and neural cascade of processes that are evoked by a stimulus or event, in particular because of the millisecond resolution of EEG recordings. In this dissertation, we took full advantage of this strength and looked at how various markers for neural and cognitive processes changed when considering multi-trial effects. We showed that to study changes in the configuration of the information processing system, it is imperative to take trial-to-trial contingencies into account (Bolt, Anderson, & Uddin, 2017). By accounting for these time-varying changes in the state of the system, we were able to map and understand the impact of prior state of the information processing system on the cascade of processes underlying the processing of future stimuli.

Although scalp-recorded EEG has significant advantages in terms of millisecond temporal resolution, one of the main disadvantages is its limited spatial resolution. The electrical brain activity measured using EEG reflects activity from billions of neurons, and disentangling the origin (i.e. which brain areas) of the scalp recorded EEG activity is difficult, especially since cognitive processes rely on multiple brain regions coordinating and influencing each other in a nonlinear fashion.

As discussed, there are numerous brain regions involved in adaptation which work together within seconds following the encountering of relevant information. A crucial next step would be to improve the spatial and temporal resolution of measurement techniques. Several promising avenues are being explored, for instance, simultaneous fMRI and EEG recordings, as well as direct current MRI, which is also known as Lorentz

effect imaging (Truong, Wilbur, & Song, 2007). Using fMRI in combination with EEG or direct current MRI is a promising avenue to expand the available toolbox for studying cognitive and neural mechanisms. In particular, being able to measure neural activity with millisecond resolution in the subcortical reward regions, and measure attentional effects in sensory regions (using for instance alpha power) would allow to test theoretical models such as proposed in this discussion. These advances in the ability to measure and combine different aspects of brain activity with increased temporal and spatial specificity is an important avenue to pursue in future research.

Reward properties of monetary incentives

The studies in this dissertation used losses and gains in points as incentives, because they are thought to influence motivation. However, importantly, participants were aware that these points would be converted to real money in the end. Our conceptualization of reward therefore is limited to that of monetary incentives. One key question is to what extent similar neural mechanisms would respond to a different type of reward, such as the prospect of food when hungry, the prospect of a cigarette when addicted, or social rewards such as approval.

In general, reward has a “liking” and a “wanting” component to it (Berridge, Robinson, & Aldridge, 2009). “Liking” refers to the hedonic impact of rewards, for instance, the pleasurable experience of eating something tasty. However, “liking” is not necessarily limited to a conscious experience; it also occurs without awareness (Winkielman, Berridge, & Wilbarger, 2005). Past literature that focused on studying the hedonic experience of rewards, such as food intake, has shown that the orbitofrontal cortices are particularly related to these pleasantness ratings of food intake (Kringelbach, 2004).

Introducing monetary incentives to the participant, mainly speaks to the “wanting” component of reward. “Wanting” is the component of rewards that is related to “approach” behavior. For instance, when seeking food, the “wanting” component of reward may refer to the motivational component of seeking food, while the “liking” component refers to the hedonic, pleasantness response of actually eating food. The studies described in the present dissertation examined the effects of reward on neural and cognitive processes mostly in terms of the ‘wanting’ component of rewards, which arguably limits our understanding of how reward can recruit attentional processes. One future direction is to study the adaptation in terms of the “liking” of rewards. For instance, by offering a prospect of different types of food as an incentive to hungry participants (taxing on liking) we would expect similar results as described in this dissertation. That is, the brain would prioritize those elements in the environment that are most “likeable”.

Taking a broader perspective: Adaptation over a lifespan

When we are born our brain contains a vast number of neurons (approximately 90 billion) and synapses (between 2500 and 10000 per neuron) (Shonkoff & Phillips, 2000). An important question is how the brain adapts its processing capabilities to the environment over a lifespan by tweaking or adjusting the connections between those neurons. That is, rather than temporary changes to the state of the information processing system, these changes will be of a more permanent nature. Below I will argue that the one answer might reside in the same mechanism, reflected by Alpha, by which attention can internalize predictive information, which, in the long-term may drive physiological changes (Kuśmierz, Isomura, & Toyoizumi, 2017).

Chapter 5 investigated how adaptation occurs from childhood until young adulthood, looking at how we learn to identify numbers and letters. While there were no observable differences in scalp recorded EEG for letters and numbers between 7 year olds and 10 year olds, by age 15, young adults showed clear separation of these two stimulus categories. From childhood to young adulthood, neural pathways seem to become specialized for the processing of letters and numbers, increasing the efficiency of information processing (Moran, Symmonds, Dolan, & Friston, 2014).

The process underlying such specialization may stem from temporary modulation of activity in specific brain areas or pathways, based on available information (e.g. feedback from the teacher when deciphering numbers or letters (P. W. Schultz, Nolan, Cialdini, Goldstein, & Griskevicius, 2007)). Although in the short term, the adaptation in the information processing system seems to rely on impacting the sensitivity of connections, these temporary changes could impact the physical connections in the long term. More specific, the synaptic connection between neurons that are activated together will become stronger (Kuśmierz et al., 2017). Our studies indeed showed that, as a result of positive feedback, the developing child's brain strengthened the connection between the configuration of lower-level stimulus features (e.g. the particular orientation and configuration of lines) and a higher-level response, indicating whether such a configuration is a letter or number, in a more permanent way.

Long-term adaptation, however, can backfire. This cost can be illustrated when the state of the system is shaped by deprivation of behaviorally relevant information (Hubel & Wiesel, 1964). In a classic experiment, Hubel and Wiesel deprived kittens of perceiving vertical lines by placing them in cylinders containing only horizontal lines, and this changed the visual system in a profound way. When, after several months, the kittens were placed back into a world which included vertical lines, they were unable respond, and could not detect vertical lines for the rest of their lives.

A key future direction is to study the relationship between potential for adaptation and aging. As most studies that use EEG to examine effects of ageing, compare young

adults (between 18 and 30 years of age) and elderly adults (60 and 80), there seems to be a gap in the literature studying adaptation across the whole lifespan. Filling this gap might form an important direction for future studies. It is possible that when we reach a certain age the brain has a more optimal model of the environment, perhaps resulting in a less adaptive but a more efficient system (Moran et al., 2014; Vaden, Hutcheson, McCollum, Kentros, & Visscher, 2012). More specifically, in the study by Vaden et al. (2012), elderly participants were less able to reduce Alpha power over those channels that would contain irrelevant information. This suggest that in elderly, we have an information processing system that has been tuned by years of experience, compared to young people, there is less of an ability to utilize behaviorally relevant information to make subtle changes in the state of the system. Because the system is very efficient and optimized for those stimuli or events that it encounters in everyday life, there is no need to be flexible anymore, perhaps an example of "use it or lose it".

Conclusion

The present dissertation aimed to elucidate those neural and cognitive mechanisms by which the brain learns from and adapts to its environment. The question that was asked was *"How do we adapt to and learn from our environment?"*. Crucially, the studies in this dissertation investigated the neural underpinnings of adaptations that are dynamic and occurs from moment-to-moment, and adaptations that are more permanent and occurs by integrating information over time. In these studies mechanisms related to attention were shown to be key to change the state of the information processing system, in particular the sensitivity to information of sensory brain regions, and influence the the priority of certain behavioral relevant information. Specifically, by modulating the neural responsiveness of brain areas involved in behaviorally relevant events or processing of stimuli based on cue and feedback information, the brain is able to adapt and learn over time.